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Komdeur, J

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No evidence for adaptive suppression of joint laying by dominant female Seychelles warblers: an experimental study

Jan Komdeur¹⁾

(Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands)

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Summary

Several theoretical frameworks exist for explaining variation in reproductive allocation between same-sex individuals living within social groups. To determine this adequately, we need to know which party is more able to manipulate reproduction of the other. Theoretical models often sidestep this problem by making the assumption that dominants either have complete or partial control of reproduction by subordinates. This study clearly indicates that in the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*) this assumption is not met. Seychelles warblers occupy year-round territories of different quality (measured as amount of insect food available). Joint laying, in which the dominant and subordinate females lay eggs in the same nest, decreases the fitness of primary females on low-quality territories, but not on high-quality territories. This study found good experimental evidence that dominant females on low-quality territories have no means to suppress or prevent subordinate females from joint laying: (i) The frequency of joint laying in multi-female groups is independent of territory quality; (ii) There is no aggression among females at the nest around the time of egg laying at either low- or high-quality territories; (iii) Dominant females do not remove the other female's egg or experimentally introduced eggs, before or after laying their own. (iv) Dominant females do not reject an experimentally introduced egg through nest desertion. Given the absence of reproductive control, increased attention to alternative models of reproductive partitioning in vertebrate societies is needed and a realistic model has to take into account interactions within the sexes.

Keywords: conflict, cooperation, cooperative breeding, joint laying, dominance interactions, subordinate, territory quality, reproductive control mechanisms, Seychelles warbler.

¹⁾ E-mail address: j.komdeur@rug.nl

Introduction

Cooperatively breeding societies contain reproducing individuals and helping individuals that assist the reproducers to reproduce. In certain cooperatively breeding vertebrates, subordinate helpers may achieve reproductive status (Rood, 1990; Taborsky, 1994; Arnold & Owens, 1998; Dierkes et al., 1999; Vehrencamp & Quinn, 2004). However, the partitioning of reproduction between group members varies greatly, both between closely related species, or within different groups of the same species (Cant & Johnstone, 1999). In many animal societies reproduction is monopolized by one or a few individuals, and potential conflicts occur over which individual(s) should reproduce (Ratnieks & Reeve, 1992). For example, conflicts over reproduction within societies are likely to occur where there are multiple adult males for every fertile female (Davies, 1992; Hrdy, 1999), or where subordinate helpers increase their fitness by becoming reproductives themselves within social groups at a cost to the fitness of the dominant (Keller & Reeve 1994; Emlen 1995, 1997, 1999; Skubic et al., 2004). Inclusive fitness theory (Hamilton, 1964) forms the basis of most models to predict the optimal reproductive strategies of different individuals within a society (Clutton-Brock, 1998; Crespi & Ragsdale, 2000). However, although theory is of great importance for understanding reproductive conflicts, it alone cannot explain the reproductive characteristics of a group. This is because theory normally indicates multiple reproductive optima, each corresponding to a different party of interest (Beekman & Ratnieks, 2003), and the theory does not tell us whose optimum will prevail or whether a compromise is being reached (Beekman et al., 2003; but see Johnstone & Cant, 1999; Johnstone, 2000). To determine this we need to know which party is more able to manipulate reproduction, in other words who has more control over reproduction (Beekman et al., 2003). Reproductive control of subordinates by same-sex dominants at a behavioural or physiological level has been documented in some studies (e.g., Reyer et al., 1986; Sherman et al., 1991; Cotgreave, 1998; Digby, 1995). Until now theory has often assumed that dominant individuals are in control of reproduction of same-sex subordinate(s) (Vehrencamp, 1983a,b; Reeve & Ratnieks, 1993; Cooney & Bennett, 2000), but this is not necessarily the case (Beekman et al., 2003; Hager & Johnstone, 2004; Langer et al., 2004; Skubic et al., 2004). Therefore theoretical predictions must be combined with an understanding of who is in control of reproduction and what mechanisms

are used to control reproduction of others (Johnstone, 2000). In this study on the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*) I investigate whether dominant females, in case where they suffer from subordinates laying eggs in the dominant's nest (joint laying), would prevent subordinate females from egg laying.

Pair-bonded adult Seychelles warblers are socially monogamous and inhabit year-round territories with the same mate (Komdeur, 1992). Although warblers can breed independently in their first year, a lack of suitable independent breeding opportunities drives some individuals into becoming subordinates, normally within their natal territory (Komdeur, 1992; Komdeur et al., 1995). Most subordinates are females (88%, Komdeur, 1996; 68%, Richardson et al., 2002; 90%, Komdeur et al., 2004) which contribute offspring care (Komdeur 1994). Breeding pairs produce one clutch per season which normally consists of just one egg (Komdeur, 1991; Richardson et al., 2001). Microsatellite-based parentage analyses demonstrated that many subordinate females gained direct parentage within the group through laying an egg in the same nest as the primary female (Richardson et al., 2002). Egg dumping between warbler groups does not occur (Richardson et al., 2002). There is two-fold evidence that the presence of female subordinates reduces the reproductive success of the primary female on low-quality territories (measured as amount of insect food available) but not on high-quality territories. First, removal of female subordinates resulted in an increase of the primary female's reproductive success on low-quality territories, probably due to reduced competition for food, and in a reduction of the primary female's reproductive success on high-quality territories due to the absence of helping behaviour (Komdeur, 1994). Second, experimental clutch enlargements from one egg to two eggs in multi-female groups showed a significant decline in recruits produced per egg on low-quality territories (no recruits from 2-egg clutches) and no change in recruits per egg on high-quality territories. The difference between the changes in number of recruits of the two groups was significant ($F = 10.93$, $df = 1$, $N = 24$, $p = 0.004$; Komdeur, 1999). Given the negative effects of joint laying on low-quality territories, primary females on these territories are expected to prevent joint laying of subordinate females.

This study was designed to answer two questions. First, is there any indication that primary female warblers on low-quality territories prevent subordinate females from joint laying? I analyse this by comparing the frequency

of one-egg (primary laid) and two-egg clutches (primary and subordinate laid) between warbler groups consisting of a primary and a subordinate female on low- and high-quality territories. Second, which control mechanism(s) are used by primary females to prevent subordinates from laying? I use groups with a primary and a subordinate female which live on low-quality territories to examine three possible control mechanisms used by primary females: aggression towards subordinates around time of egg laying to prevent subordinate from access to the nest, nest desertion after subordinate laying in the same nest, or tossing of the subordinate's egg. The last two mechanisms were examined experimentally by simulated joint laying in which a model egg was added just before egg laying using the natural time window of joint laying.

Material and methods

Study site and population monitoring

The Seychelles warbler is a rare island endemic which, until 1988, was restricted to Cousin Island (29 ha) in the Seychelles. The entire population of warblers on Cousin has been monitored intensively since 1985. During this time, most birds (>96%; adults and nestlings) were individually colour-ringed (using a unique combination of three colour rings and a British Trust for Ornithology metal ring) and monitored throughout breeding attempts. Therefore, the reproductive history, putative pedigree and status of the majority of birds are known. Seychelles warblers were sexed using molecular techniques (Griffiths et al., 1998). Behavioural observations were used to determine the status of all birds within each territory. The 'primary' male and female were defined as the dominant, pair-bonded male and female in the territory, while the term 'subordinate' included all other adult birds (>8 months old) resident in the territory (Richardson et al., 2002). During the breeding seasons in each year the quality of all territories was measured monthly. Seychelles warblers are insectivorous and so territory quality was expressed as the mean number of prey invertebrates available within a territory (for methods, see Komdeur, 1991, 1994). Territories were divided into three territory quality categories: low (0-1,500 insects present in a territory), medium (1,501-3,000 insects), or high quality (>3,000 insects).

The present study was based on the Seychelles warblers studied between May – September (the main breeding season) in 1995 and 1996. In total 54 warbler territories were randomly selected at the beginning of each breeding season (29 in 1995, 25 in 1996) which varied in quality and number of females present; 31 low-quality territories (10 with a breeding pair, 21 with a breeding pair and a subordinate female) and 23 high-quality territories (8 with a breeding pair, 15 with a breeding pair and a subordinate female). Each of these territories were checked weekly for initiation of nestbuilding by following the primary female for 30 min because the female alone is involved in nestbuilding (Komdeur, 1992). Of the 54 breeding groups monitored, 51 groups produced a nest. All nests were found during the nest building phase ($N = 51$). During this period, which lasts up to 19 days (Komdeur, 1991), nests were checked daily for the presence of egg(s), where necessary with the help of a mirror attached to a stick. The days of the observation period are numbered backward from the start of laying, i.e. day -4 was four days before the first egg was laid. Immediately on finding an egg, the egg was numbered with a permanent marker.

Observations of aggressive incidents between primary female and subordinate female were recorded during two periods: a 4-day period starting 4 days before egg laying until the day of laying the first egg and a 4-day post-laying period which started on the day of laying of the first egg. The 4-day pre-laying period is assumed to be the fertile period of the primary female, because copulations only take place during this period (Komdeur et al., 1999). The onset of the 4-day pre-laying period was determined as the day at which the primary female began lining the nest (Komdeur et al., 1999). Aggressive incidents were measured when the primary and subordinate females were simultaneously present within a 2.5 m radius from the nest. The nests were observed from 0700–1000 h until I had 10–20 independent cases of females being simultaneously present close to the nest for each of the two four-day periods. When aggressive incidents occurred, it was noted which bird chased which.

Experimental simulation of joint laying

To test whether primary females on low-quality territories use either nest desertion or egg ejection as a control mechanism, I simulated joint laying experimentally on 12 low-quality territories with a primary and subordinate female by placing a model Seychelles warbler egg in the empty nest

during the fertile period of the primary female. The employed experimental procedure is adequate because in principle primary females might have evolved nest desertion or egg ejection as control mechanisms. In cases of joint laying where females laid on different days and with eggs marked immediately upon laying and sampled at a later stage for parentage analyses, in 44% (4/9) of cases the subordinate laid before the primary female laid her own egg (J. Komdeur, D.S. Richardson, T. Burke, unpubl. data). The model eggs were made of wax and painted with a waterproof marker to match the pattern of real warbler eggs. In another experiment it was shown that Seychelles warblers perceive model eggs as real conspecific eggs (Komdeur et al., 1999). The standard model egg measurements (length: 20.0 mm; width: 14.0 mm; mass: 2.0 gr) were within the natural range of Seychelles warbler eggs (length: 20.0 ± 0.9 mm; width: 14.0 ± 0.5 mm; mass: 2.2 ± 0.2 gr, $N = 36$). Model eggs were placed during the early morning to mimic the laying time of real eggs, and before egg laying started allowing the primary female to reject the egg without rejection costs. A rejection cost can occur through accidental rejection of the primary female's own egg instead of the parasitic egg, or through the primary female accidentally damaging her own egg(s) along with the parasitic egg (Davies & Brooke, 1988). As a control, I performed the same actions around the nests of 9 groups comprising a primary and subordinate female on low-quality territories, but without the addition of a model egg. Control and experimental nests were disturbed in the same frequency (checked daily) and for the same duration. Control and experimental treatments were randomly assigned to nests. On the day(s) following the treatments the nests were monitored daily for presence or absence of the model and numbered real egg(s), and observed daily for 30 min for nest desertion (no activity around nest). In cases where eggs were laid, observations continued until four days after laying of the last (real) egg. In the nests containing a model egg, a real egg was laid 1 ($N = 4$), 2 ($N = 3$), 3 ($N = 1$) or 4 ($N = 4$) days after the addition of the model egg. One day after the addition of the model egg, the experimental nests which did not contain a real egg ($N = 8$) were observed for 30 min for incubation activity. A female was defined as incubating when the average time bout spent on the nest was more than 10 min (Komdeur, 1991). The identity of the incubating female(s) was also noted.

Data analyses

Focal-group observations in 1995 and 1996 involved different groups to avoid duplications. Observations were coded in relation to the laying of the first egg (day 0). For each primary female in groups with a subordinate female present I determined the number of subordinate chases during the observation period (expressed as frequency per hour) and I calculated a mean daily frequency value of aggressive incidents across all groups from day -4 to day -1, and from day 0 to day 3. I defined the occurrence of joint laying in multi-female groups as the presence of a two-egg clutch for the following reason: egg dumping between warbler groups is absent (Richardson et al., 2002), and primary females normally lay one-egg clutches when breeding in pairs (Komdeur, 1991; Richardson et al., 2001; see results below), and when breeding in groups primary females do not lay larger clutches in anticipation of help from subordinate females (Komdeur 1991, 1994). Because average clutch size was either one or two (see results below), logistic regression was used to test the effect of multiple independent terms on clutch size. Furthermore, because average clutch size was not affected by the addition of a model egg (see results below), I pooled the nests with and without model eggs. As predictors for clutch size, I used number of females present, date of laying, territory quality, and year of study. Potential explanatory terms and two-way interactions were fitted using the stepwise backward removal of non-significant terms. Year of breeding and territory quality were entered as a categorical term; other terms were entered as covariates. Because none of the two-way interactions were significant, these were left out in the results section. The Wald test statistic is given. Statistical analyses were performed using SPSS v. 11.0 (SPSS, 2001). Probability values are two-tailed and the null hypothesis was rejected at $p < 0.05$.

Results

Factors determining clutch size

Of the 54 breeding groups monitored, 94% (51 groups) produced a nest and 93% (50 groups) produced a clutch. The presence of a subordinate female had a significant positive effect on the chance of groups producing a clutch; 77.8% of breeding pairs ($N = 18$) and 100% of breeding pairs with a subordinate female ($N = 36$) produced a clutch (General Linear Model with

Table 1. Logistic regression analyses of the effects of variables on the incidence of single-egg ($N = 35$) or two-egg clutches ($N = 15$) in Seychelles warbler territories (14 territories with a primary female, 36 territories with a primary and one subordinate female (1995-1996)). The presence of a subordinate female was the only variable left in the minimal adequate model after stepwise removal of non-significant variables.

Incidence of two-egg clutches			
Explanatory terms	Wald	df	<i>p</i>
Presence subordinate female	5.768	1	0.016
Year	0.632	1	0.427
Territory quality	0.184	1	0.668
Laying date	-2.394	1	0.122

binomial errors, $Wald = 8.64$, $df = 1$, $p = 0.003$; Figure 1a). However, the chance of groups producing a clutch was not associated with territory quality; 97% (28/29) of groups in low-quality and 88% (22/25) of groups in high-quality territories produced a clutch ($Wald = 1.43$, $df = 1$, $p = 0.232$; Figure 1a). Clutch size was either one (70% of clutches) or two (30% of clutches). Two lines of evidence indicate that there was joint laying in our population rather than one female producing two eggs: (1) The frequency of two-egg clutches was significantly affected by the presence of a subordinate female (Table 1; Figure 1b). Groups comprising a breeding pair and a subordinate female produced two-egg clutches significantly more often than breeding pairs without subordinates (percentage two-egg clutches: 39% (14/36) and 7% (1/14), respectively; see Table 1; Figure 1b). The frequency of two-egg clutches was not associated with territory quality (percentage two-egg clutches: 32% (9/28) on low- and 27% (6/22) on high-quality territories; Figure 1b), the date of egg laying, or the year of study (Table 1). (2) In 4 out of the 22 two-egg clutches produced in multi-female groups, both eggs were laid on the same day in a single nest, whereas in the single case of a two-egg clutch produced by a single female group eggs were laid one day apart. Given that the frequency of two-egg clutches (joint laying) in groups of two females is equal on low- and high-quality territories it seems that primary females do not prevent subordinate females from laying.

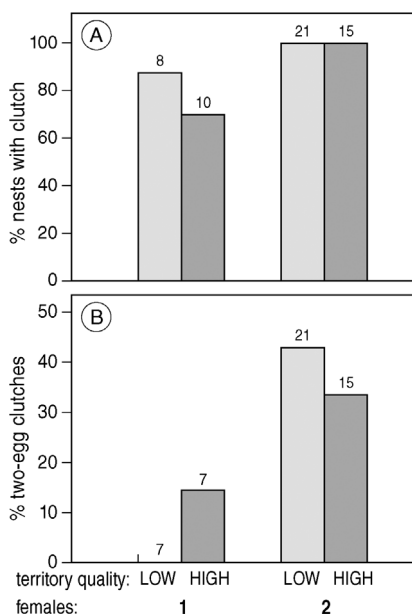


Figure 1. (A) Percentage of Seychelles warbler breeding groups producing a nest with a clutch in relation to number of females present in groups and territory quality. Figures indicate number of groups (1995-1996). (B) Percentage of clutches containing two eggs (clutch size was either one or two) in relation to number of females present in groups and territory quality. Figures indicate number of groups producing one clutch each (1995-1996).

Control mechanisms of subordinate egg laying

Primary females on low-quality territories do not seem to exert control over subordinate laying. This is supported by three findings. (i) No aggressive incidents between the primary female and subordinate female were observed during the pre-laying and post-laying periods on either low-quality territories (mean cases per territory of females being simultaneously present within 2.5 m radius from the nest: pre-laying: 14.0; post-laying: 15.9; $N = 21$ territories) and high-quality territories (mean cases per territory of females being simultaneously present within 2.5 m radius from the nest: pre-laying: 18.2; post-laying: 16.6; $N = 15$ territories). (ii) The model egg addition experiments showed that primary females on low-quality territories readily accept eggs. None of the focal primary females deserted the nest containing a model egg. In all 12 cases a real egg was laid after introduction of the model egg. In 42% (5/12) of cases the primary female and in 25% (3/12) of cases the subordinate female were observed incubating the model egg

before egg laying had started, and in 17% of cases (2/12) shared primary-subordinate female incubation of the model was observed. (iii) Furthermore, none of the model eggs or real eggs were ejected through tossing. In all nests (12/12) the model egg remained in the nest either before or after egg laying. Correct egg tossing could have occurred in all 12 nests in which the model egg was added before egg laying started. The addition of a model egg during nestbuilding had no effect on average number of eggs laid (mean clutch size experimental versus control groups: 1.4 ± 0.2 ($N = 12$) vs 1.4 ± 0.2 ($N = 9$); $\chi^2 = 0.016$, $df = 1$, $p = 0.899$).

Discussion

Joint laying and behavioural mechanisms to prevent subordinate reproduction

Communal laying is a relatively rare form of avian cooperative breeding in which two or more breeding group members of the same sex contribute genes to a clutch of eggs and cooperate in the care of young (Brown, 1987; Vehrencamp, 2000; Vehrencamp & Quinn, 2004). In some species the incidence of female subordinate egg-dumping is extremely rare (for example the Florida scrub-jay, *Aphelocoma coerulescens*; Quinn et al., 1999), while in others it is low but persistent, occurring in the order of 10% of nests (Vehrencamp, 2000). In contrast, the incidence of two-egg clutches (indicative of joint laying by primary and subordinate female) in the Seychelles warbler in this study was high, occurring in 39% of nests, and was similar on either low- and high-quality territories. The latter suggest that primary females do not exert full direct control of egg laying by subordinate females, given that experimentally simulated joint laying on low-quality territories comprising a primary and a subordinate female decreased the fitness of primary females (Komdeur, 1999). This study found good evidence that primary females do not exert active control over reproduction by subordinates. (i) The frequency of two-egg clutches in multi-female groups is independent of territory quality. (ii) There is no aggression among females at the nest around the time of egg laying at either low- and high-quality territories. In meerkats (*Suricata suricatta*) dominant females in larger groups do not gain by having reproducing subordinates in the group. However, the amount of primary-subordinate female aggression is independent of group size, and subordinate females in large

groups are no more expelled or restrained from breeding than subordinates in small groups (Clutton-Brock et al., 2001). In oystercatchers (*Haematopus ostralegus*) joint nesting dominant females have lower reproductive success than solitary breeding females. However, aggression between females around the time of egg laying and egg tossing were not observed (Heg & Treuren, 1998). (iii) Primary females do not remove the other female's egg or experimentally introduced eggs, before or after laying their own. In other species, as in the communally breeding ostrich (*Struthio camelis*; Bertram, 1992) and the closely related Australian warbler (*Acrocephalus australis*; Welbergen et al., 2001), females can recognize their own eggs and expel eggs laid by other females. Even if a female cannot distinguish between her own and another female's egg, she could use the presence of an egg before laying her own as a cue that that egg must have been laid by another bird. In principle, primary females might have evolved egg ejection as a control mechanism, because in 44% of cases of joint laying subordinates lay first (J. Komdeur, D.S. Richardson, T. Burke, unpubl. data). However, Seychelles warbler females do not remove the experimental egg already present in the nest when they themselves have not begun laying. In some cases females began incubating the experimental egg before laying their own. In contrast, primary and subordinate female acorn woodpeckers (*Melanerpes formicivorus*; Koenig et al., 1995), groove-billed anis (*Crotophaga ani*; Vehrencamp & Quinn, 2004) and guira cuckoos (*Guira guira*; Macedo et al., 2004) remove eggs from a communal nest until they themselves start laying. (iv) Primary female Seychelles warblers do not reject the experimentally introduced egg through nest desertion.

Non invasive control mechanisms of subordinate reproduction

Under special conditions, in groups comprising several adults of the same sex, the dominants can gain the largest share of reproduction without even having to exert power, for example, when the need for inbreeding avoidance limits the opportunities for subordinates to mate (Beekman et al., 2003; Russell, 2004). When inbreeding is deleterious and the group comprises close relatives, subordinates should not mate and produce with the dominant individual (Emlen, 1996). With no other mating opportunities available, monopolizing breeding is an easy victory for the dominant individuals (Coony & Bennett, 2000; Koenig et al., 1998; Faulkes & Bennett, 2001; Clutton-Brock

et al., 2001). In the highly inbred Seychelles warbler where close inbreeding is deleterious for the offspring produced, subordinate breeding is not constrained by close inbreeding (Richardson et al., 2004). The frequency of female subordinate breeding is independent of genetic relatedness to the males present in the group. The subordinate females avoid close inbreeding by producing more extra-group young (sired by less related males from outside the group) when she is more closely related to the group male(s) (Richardson et al., 2004).

Another control mechanism is biasing offspring sex ratio. The Seychelles warbler is atypical in cooperative breeding birds in that it has male dispersal and female-biased helping (Komdeur, 1992, 1996). Breeding pairs on high-quality territories gain higher reproductive success from keeping subordinate females, but breeding pairs on low-quality territories lose in their own productivity in case of tolerating female subordinates (Komdeur, 1994, 1999). This study shows that primary females on low-quality territories do not use direct control mechanisms to limit the presence and joint laying of female subordinates. However, since in birds females are the heterogametic sex (ZW) and determine the sex of their eggs, egg sex modification may be used as a control mechanism that anticipates the negative or positive effects of future remaining female subordinates. Seychelles warbler primary females adaptively modify the sex of their single-egg clutch towards daughters (88% of eggs), the remaining sex, when living on high-quality territories but toward sons (77% of eggs), the dispersing sex, when living on low-quality territories (Komdeur et al., 1997). This resulted in more groups consisting of one or more adult males and one adult female on low-quality territories than on high quality territories (percentage single-female groups (1994-1996): 83% (127/153) and 46% (25/54), respectively; $\chi^2 = 25.66$, $df = 1$, $p < 0.001$). This species represents an unusual example of egg sex modification as a control mechanism for foreseeing the negative effects of future female subordinates. The advantage for a subordinate female staying on a high-quality natal territory is attaining breeding status through joint nesting, thereby increasing the benefits of philopatry by reducing the length of time elapsing before she could reproduce (Heg & Treuren, 1998).

Concluding remarks

Several theoretical frameworks exist for explaining variation in reproductive allocation between same-sex individuals living within social groups. To de-

termine this adequately, we need to know which party is more able to manipulate reproduction of the other. Theoretical models often sidestep this problem by making the assumption that dominants either have complete control of reproduction by subordinates (e.g., Vehrencamp, 1983a,b; Reeve & Ratnieks, 1993; Cooney & Bennett, 2000), or have no full control of subordinate reproduction (e.g., Johnstone & Cant, 1999; Johnstone, 2000; Hamilton, 2004; Skubic et al., 2004). This study clearly indicates that in the Seychelles warbler primary females have no complete control of reproduction by subordinate females. Primary females do not apply behavioural mechanisms to prevent subordinates from joint laying in situations when suppression of subordinate production would be adaptive. Therefore increased attention to alternative models of reproductive partitioning in vertebrate societies is needed and a realistic model will have to take into account interactions within the sexes. Although the data on joint nesting in this study are estimates based on the frequency of two-egg clutches, molecular parentage analyses should be used to determine exactly the frequency of individual reproduction and reproductive sharing for primary and subordinate females.

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